REVIEW/SYNTHÈSE

A discussion of microstructural changes in wood during decomposition by white rot basidiomycetes[1]

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The classical concepts of wood decay are reviewed. All white rot fungi do not cause the same type of cell wall decomposition. At least two micromorphologically distinct types of cell wall attack have been found. Many factors can affect the type of macroscopic and microscopic decay patterns caused by white rot basidiomycetes. Host cell type and nutrients, as well as genetic and physiologic differences among these fungi, may influence the resulting decay.

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Les auteurs présentent une revue des concepts concernant la carie du bois. Tous les champignons responsables de caries blanches ne causent pas le même type de décomposition des parois cellulaires. Il y a au moins deux types micromorphologiques d'attaque des parois cellulaires. Plusieurs facteurs peuvent affecter les types de patrons macroscopiques et microscopiques de caries causées par les basidiomycètes responsables de la carie blanche. Le type de cellule hôte, les nutriments ainsi que les différences génétiques et physiologiques parmi ces champignons peuvent influencer les caries qui en résultent.

[Traduit par la Revue]

Introduction

Of the fungi that inhabit the forest floor, basidiomycetes are the most important in recycling the carbon stored in wood. White rot basidiomycetes are especially important in the forest ecosystem since they are the only fungi capable of degrading all cell wall components (cellulose, lignin, hemicelluloses) of wood. Some white rot basidiomycetes, however, will selectively remove lignin from wood and leave most of the cellulose behind (Blanchette 1984*c*). Currently, there has been interest in fungi with this ability because of their potential for industrial use (Eriksson 1985; Kirk et al. 1980). The cellulose fiber which is left by these fungi could be used for making paper, fed to ruminant animals as a carbohydrate source, or broken down and fermented to produce ethanol or other valuable biochemicals. New information suggests that some white rot fungi are capable of switching from a degradative system that selectively removes lignin to a system that simultaneously removes all cell wall components (Blanchette 1984*a*; Blanchette et al. 1985). The ability of a single white rot fungus to cause two micromorphologically distinct types of cell wall degradation suggests that the decay capacities of white rot fungi need to be reevaluated using new techniques. It is important to understand the different capacities that white rot fungi have for degrading wood and the factors responsible for causing different degradative processes. Only then can a more accurate concept of wood decomposition be realized and the ultimate goal of using these fungi for industrial purposes be achieved.

Classical wood decay concepts

Research in wood decay began in Europe with the discoveries by Robert Hartig before the turn of the 20th century. Hartig (1878) separated the white rots from the red rots (now known as brown rots) by the color of decayed wood. Falck (1926) was the first to show the basic chemical changes that accompanied white rots and brown rots. White rot fungi removed lignin and cellulose, whereas brown rot fungi removed only cellulose. Bjorkman et al. (1949) separated the white rot group into two categories. Some white rot fungi were found to remove all cell wall components simultaneously, while others were found to remove lignin and hemicelluloses first leaving the cellulose. He identified the categories as white rot and corrosive rot, respectively. Meier (1955) described these differences in greater detail using electron microscopy. He renamed the decay categories of white rot fungi as simultaneous rots (Bjorkman's white rots) and white rots (Bjorkman's corrosive rots). The different uses for the term "white rot," however, have caused confusion. Hartig, Bjorkman, and Meier all defined the term differently. This change in nomenclature was eased when members of the European scientific community accepted Meier's definitions. Liese (1970) reviewed the differences between these two types of rot and corrected some of the confusion.

Hubert (1931) and Boyce (1961) in the United States separated the white rots, as Hartig had described them, from the brown rots and recognized differences among white rots. However, no attempts were made to separate the fungi that selectively degraded lignin from simultaneous rotters. The early forest pathologists were concerned primarily with the macroscopic appearances of decayed wood for identification purposes. As a result, decay was categorized as white-pocket rot, white-mottled rot, white-spongy rot, white-stringy rot, etc. Field observations and detailed microscopic evaluations were made during this period of research (von Schrenk and Spaulding 1909; Hubert 1924). As the chemical aspects of wood decay were investigated, a small number of fungi were selected for laboratory observation and thus became models for the categorization of decay types. Throughout most of these studies the same organisms were used. In the United States, Cowling (1961) and Wilcox (1968) characterized the microscopic and chemical aspects of white rot using *Coriolus versicolor* (L. : Fr.) Quél. By narrowing their focus to one fungus (which caused a simultaneous rot), other researchers assumed that all white rot fungi degraded wood in a similar fashion and

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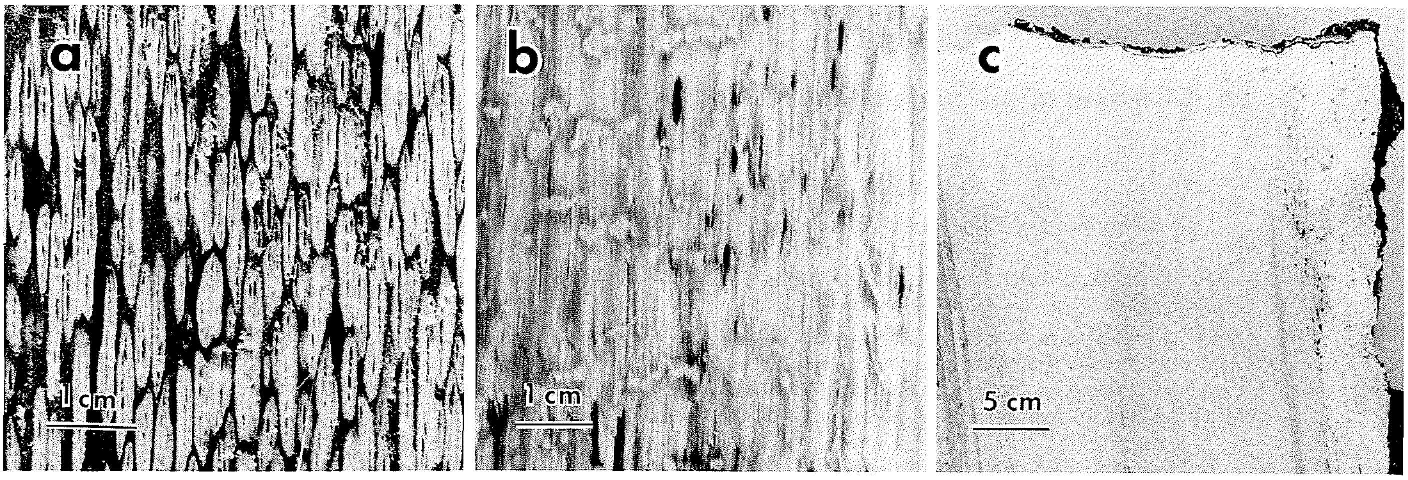

FIG. 1. (*a*) Pocket rot in *Larix occidentalis* Nutt. decayed by *Phellinus pini*. (*b*) Mottled decay pattern of *Betula papyrifera* caused by *Ischnoderma resinosum*. (*c*) Uniform white rot in *Betula papyrifera* caused by *Coriolus versicolor*.

that a gradation merely existed in their specificity toward lignin degradation (Seifert 1968). In Europe, *C. versicolor* decay typified the simultaneous rot, and *Phellinus pini* (Thors : Fr.) Pilát decay typified the selective delignification in Meier (1955) and Liese's (1970) work. By also making generalizations based on observations of wood decayed by only a few fungi, concepts of wood decay were skewed to indicate that all white rot fungi could fit into one of the categories described. In Meier's study (1955), *Trametes radiciperda* (*Heterobasidion annosum* (Fr.) Bref.) caused a simultaneous rot of spruce wood (*Picea excelsa* Link) in the laboratory and a selective delignification of birch wood (*Betula verrucosa* Ehrh.) in the laboratory. *Heterobasidion annosum* was classified as a simultaneous rot in Meier's publication. In the forest, however, *H. annosum* has been found to cause both a simultaneous rot and a selective delignification within stumps of *Pinus resinosa* Ait. (Blanchette 1984*c*). Current research (Blanchette et al. 1985) suggests that the types of decay caused by many white rot fungi do not fit into the classical categories established for wood decay.

Variation in wood decay caused by white rot fungi

In natural forest ecosystems, decayed wood can have a myriad of macroscopic appearances and textures. White-pocket rot, white-mottled rot, and a uniformly bleached white rot (Figs. 1*a*−1*c*) represent some of the decay patterns possible. White-pocket rot fungi usually cause a selective delignification in localized areas of wood (Fig. 2*a*) but also have been shown to cause a combination of simultaneous rot and selective delignification (Fig. 2*b*). Other white-pocket rot fungi have the ability to remove the cellulose that remains after removing lignin from the wood (Figs. 2*c*, 2*d*). The mottled appearance of some white rots can be caused by localized areas of abundant hyphae (Figs. 3*a*−3*c*) or selectively delignified wood interspersed among areas of simultaneously rotted wood surrounding hyphal masses (Figs. 4*a*−4*f*). Wood that was uniformly white rotted usually resulted from the simultaneous removal of all cell wall components either directly around the fungal hyphae causing erosion troughs and holes (Fig. 5*a*) or by an overall thinning of the cell walls from the lumen toward the middle lamella (Fig. 5*b*).

The macroscopic decay patterns observed in advanced stages of decay resulted from an interaction between fungi and their substrates. The anatomy of the host and cell wall structure of various cell types have been shown to be factors in determining the decay patterns that occur, particularly among fungi that selectively delignify wood. Some fungi selectively delignify only part of an annual ring. For example, *Ganoderma tsugae* Murr. preferentially delignified the earlywood cells of *Tsuga canadensis* (L.) Carr. but caused a simultaneous rot in areas of latewood (Fig. 5*c*). *Phellinus pini* preferentially attacked the latewood cells of *Larix occidentalis* Nutt. (Fig. 5*d*), and *Inonotus dryophilus* (Berk.) Murr. selectively delignified only the axial parenchyma cells in oak (*Quercus alba* L.) (Fig. 5*f*). One common observation of selectively delignified wood is that uniseriate rays are often completely removed (Fig. 2*a*). It seems probable that white rot fungi differ in their ability to decay wood as a result of differences in types of enzymes produced and how these enzymes are able to act upon the specific organization of cell wall components. Selective delignification has been found to occur only in localized areas of wood (e.g., earlywood, latewood, parenchyma cells, etc.). Fungi that cause a simultaneous rot appear less affected by cell wall structure since this type of decay usually occurs throughout all cell types within a host (Fig. 5*e*).

There are some exceptions in that not all fungi that selectively delignify wood are restricted by cell type. Some white-pocket rot fungi are able to selectively delignify most cell types within the wood. Reasons for the localized delignification caused by these fungi vary. *Xylobolus frustulatus* (Pers. : Fr.) Boid. appears to be restricted by the accumulation of polymerization products during decomposition (Otjen and Blanchette 1984). *Hirschioporus pargamenus* (Fr.) Bond. and Sing. produces a network of interwoven hyphal webs between pockets of delignified wood that appear to inhibit the delignification process (Otjen 1985).

Some fungi, such as *Ischnoderma resinosum* (Fr.) Karst., can cause a selective delignification and a simultaneous rot within the same birch log (*Betula papyrifera* Marsh.). Henningsson et al. (1972) also noted that a single species of *Peniophora* could cause two types of cell wall attack within birch wood decayed in the laboratory. Reasons for this type of variation in decay capacity apparently include more than differences in cell wall structure within the host.

Large amounts of mycelium, surrounded by simultaneous white-rotted wood, are commonly associated with mottled

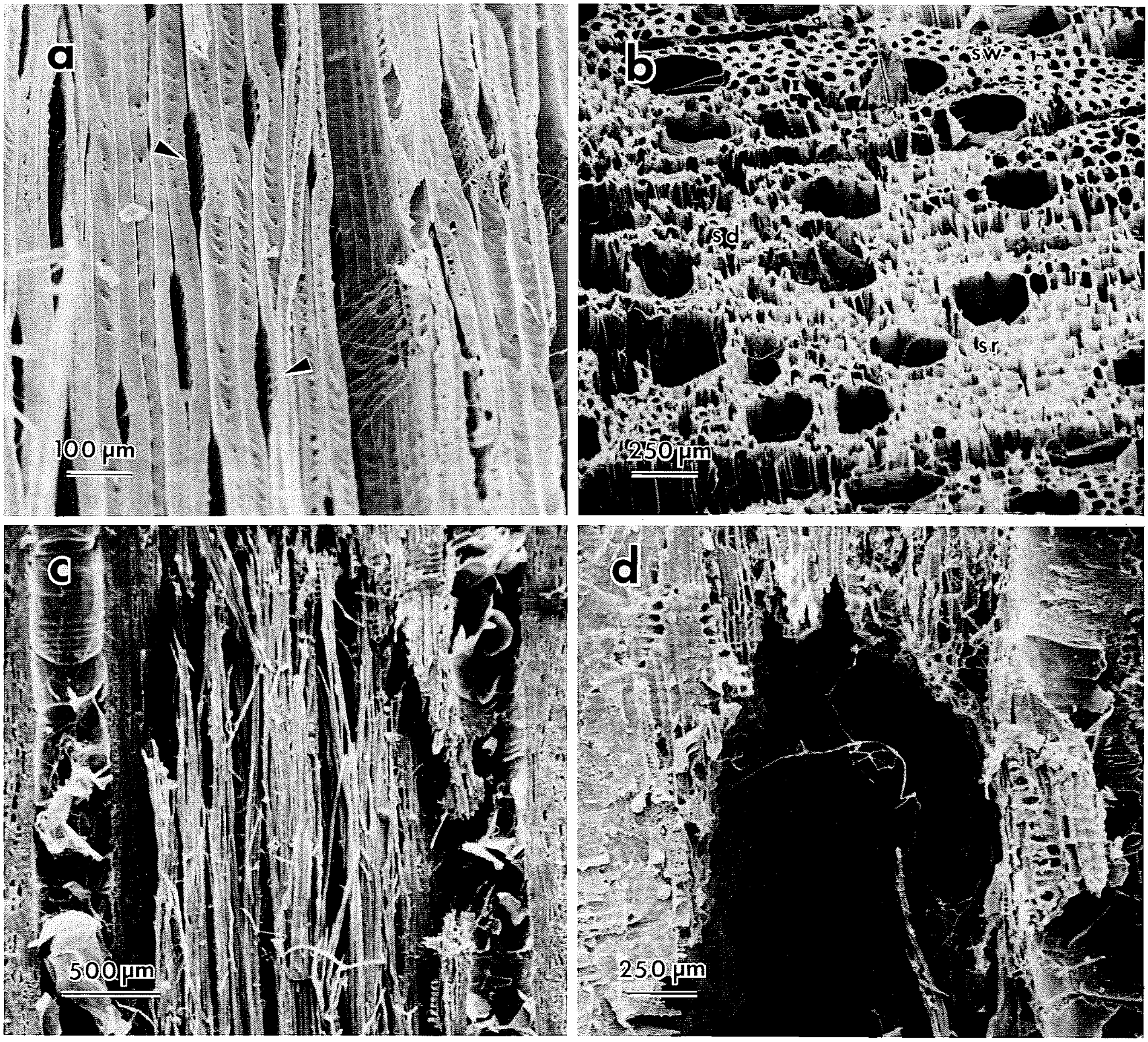

FIG. 2. (*a*) Selectively delignified *Pinus monticola* Dougl. wood void of ray cells (arrowheads) in pockets decayed by *Phellinus pini*. (*b*) Transverse section of a white-pocket rot of *Betula papyrifera* caused by *Hirschioporus pargamenus* displaying zones of selective delignification (*sd*), simultaneous rot (*sr*) and sound wood between pockets (*sw*). (*c*) White-pocket rot in *Quercus alba* selectively delignified by *Xylobolus frustulatus* during incipient stages of decay. (*d*) Empty pocket left after *Xylobolus frustulatus* removed the cellulose.

rots. These areas occur within larger areas of selectively delignified wood. It is not known why areas of lignified wood remain adjacent to delignified cells. The consistent separation of selectively delignified wood from simultaneously rotted wood suggests that the simultaneously rotted wood is somehow altered so that it cannot be selectively delignified. Simultaneous rot has also never been observed to follow selective delignification (Blanchette 1984*a;* Blanchette et al. 1985). Physiological differences between hyphae in selectively delignified wood and the masses of mycelium in the simultaneously rotted wood appear to exist. All cell wall components of simultaneously rotted wood are removed directly around fungal hyphae. Voids formed in the wood by the removal of all cell wall material are filled with mycelium. In selectively delignified wood, hyphae are very sparse and lignin and hemicelluloses are selectively removed leaving cellulose behind in the form of macrofibrils. The process of selective delignification occurs at a distance from fungal hyphae (Blanchette 1984*b*; Blanchette et al. 1985; Otjen and Blanchette 1982) indicating that a diffusible lignin degrading system is produced.

Differences have been noted between white-rotted and selectively delignified wood. High accumulations of Mn oxides within some delignified areas of wood (Blanchette 1984*b*) and the higher pH of delignified wood (L. Otjen and R. A. Blanchette, unpublished data) are two of the most noted changes. The effects of various elements and altered pH on the process governing control of selective delignification are phenomena worthy of additional study.

When basidiomycetes produce sporophores, endocellulase production can increase up to 10-fold (Wood and Leatham 1983) and stored nutrients are transported to the wood surface for sporophore production (Gruen and Wu 1972). Mycelium in

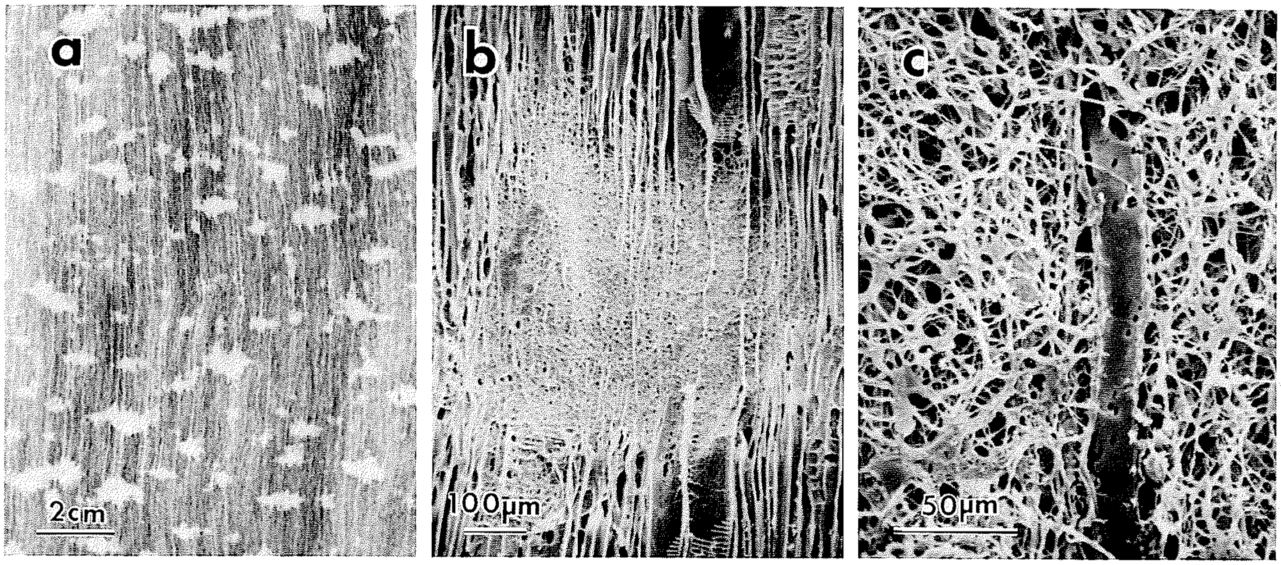

FIG. 3. Decay of *Populus deltoides* Michx. by *Ischnoderma resinosum*. (*a*) Macroscopic view of decayed wood containing irregular white patches. (*b* and *c*) Scanning electron micrographs of a white zone showing that they are composed of fungal mycelia. Degraded areas, caused by a typical white rot attack, coalesced to form voids filled with mycelia.

wood decayed by many white rot basidiomycetes creates a network, radially and circumferentially aligned in the wood. These interconnected zones of mycelium appear to act as a transport system to the log surface. Since selectively delignified wood contains sparse amounts of hyphae, there would be inadequate storage of nutrients for sporophore production if a fungus, such as *I. resinosum*, selectively delignified all of the wood. The areas of white rot within zones of delignified wood appear to act as reserve areas for carbohydrate storage and translocation of nutrients used during reproduction.

There is evidence to suggest that some genetic control exists over the type of decay a single species of white rot basidiomycete may cause. For example, *Cerrena unicolor* (Fr.) Murr. can decay downed birch as well as cause a canker of living birch trees. All isolates which have been found to cause a canker also cause a simultaneous rot. Isolates from birch which were not associated with cankers, however, have been found to cause a combination of selective delignification and simultaneous rot (L. Otjen and R. A. Blanchette, unpublished data). This situation also has been demonstrated for a variety of *Phellinus pini* (*P. pini* var. *cancriformans*) in white fir (Blanchette 1982). It seems likely that white rot basidiomycetes with the ability to cause two types of cell wall degradation can give rise to isolates that cause only a simultaneous rot. The varied decay patterns observed in wood decayed by a single species of basidiomycete could be due to variation within that species.

White rot basidiomycetes vary greatly in their ability to cause different micromorphological patterns of decay. Individual white rot fungi can cause different types of decay in different cell types within a host. The reasons for these differences are many-fold and have been outlined. Researchers need to recognize that different white rot fungi have varied capacities of removing lignin, cellulose, and hemicelluloses from wood. Prior to application of white rot basidiomycetes for industrial use, knowledge of how these fungi degrade different cells and the processes responsible for the degradation is necessary.

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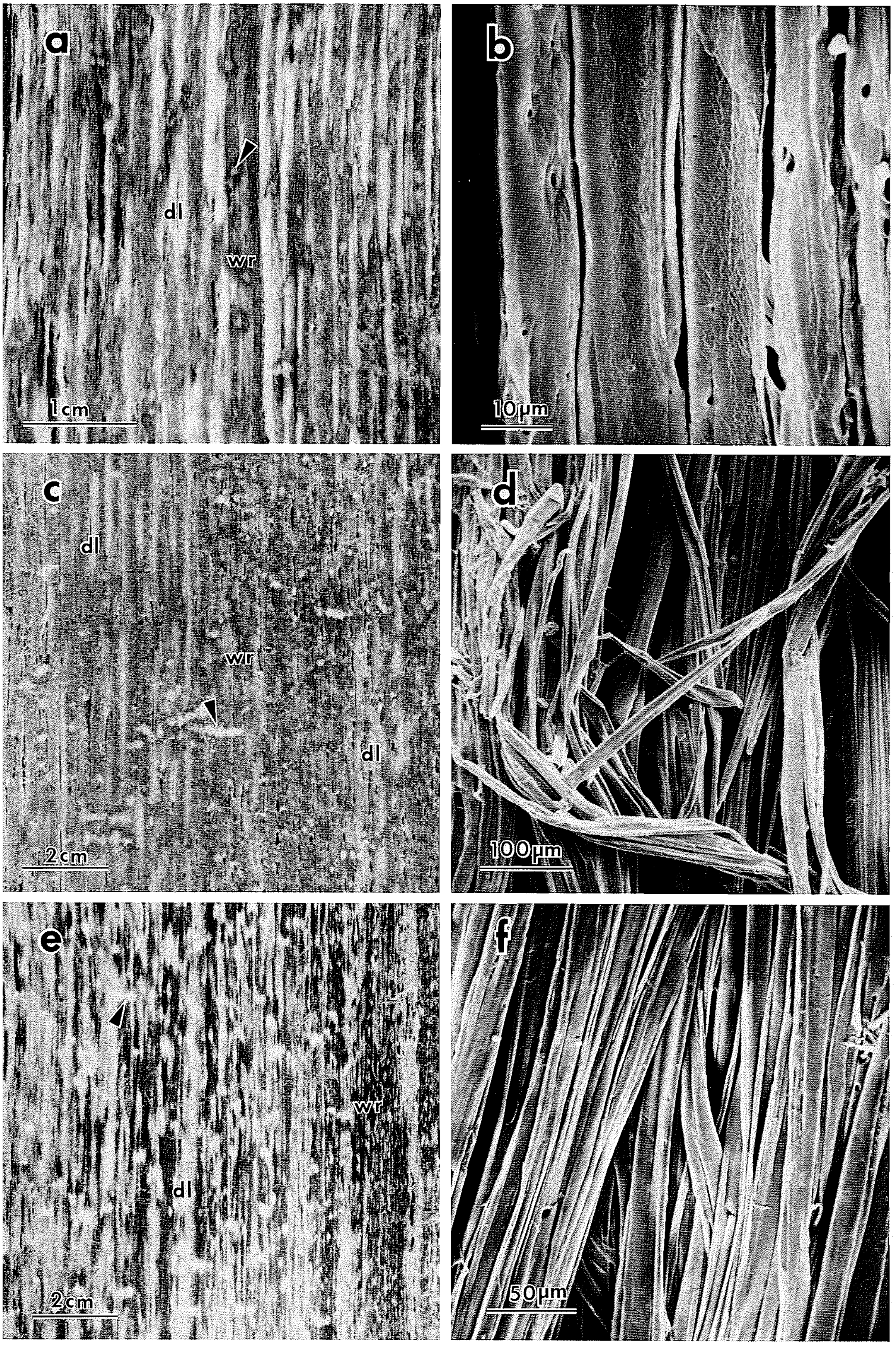
FIG. 4. *Betula papyrifera* decayed by (*a* and *b*) *Cerrena unicolor*, (*c* and *d*) *Ischnoderma resinosum*, and (*e* and *f*) *Poria medulla-panis*. (*a,c,e*) Macroscopic observations of decayed wood showing white delignified areas (*dl*) and yellowish or tan-colored white-rotted wood (*wr*) with white mycelia filling voids within the white-rotted wood (arrowheads). (*b,d,f*) Scanning electron micrographs of delignified areas (from area *dl* in Figs. 4*a*, 4*c*, 4*e*), showing a separation of cells due to lack of middle lamellae.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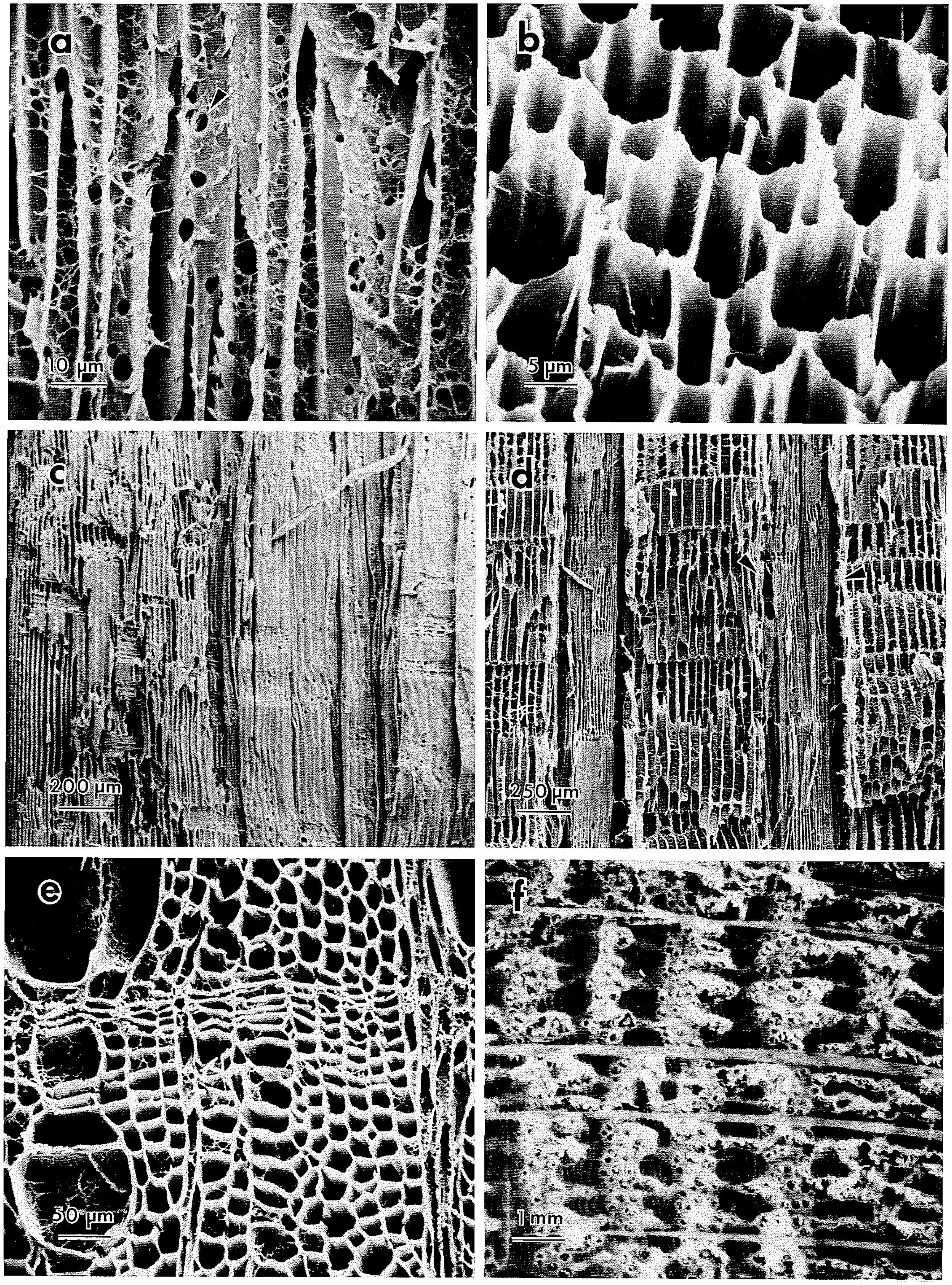
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FIG. 5. (*a*) Degradation of all cell wall components directly around hyphae of *Phellinus tremulae*, causing holes in cell walls of *Populus tremuloides*. (*b*) Uniform removal of all cell wall components from the lumens outward, causing a thinning of cell walls by *Phellinus gilvus* in *Quercus rubra* L. (*c*) Selective delignification of *Tsuga canadensis* earlywood cells by *Ganoderma tsugae*. (*d*) Selective delignification of latewood cells by *Phellinus pini* in *Larix occidentalis*. (*e*) Simultaneous rot of *Betula papyrifera* by *Cerrena unicolor* occurring uniformly in earlywood and latewood. (*f*) Axial parenchyma cells of *Quercus alba* selectively delignified by *Inonotus dryophilus*.